

SHORT COMMUNICATION

VARIATIONS IN WEB CONSTRUCTION IN *LEUCAUGE VENUSTA* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. The distribution of female *Leucauge venusta* (Walckenaer 1841) in a coffee plantation in southern Mexico was studied in order to determine the vertical distribution of this spider. Principal component analysis clearly identified the presence of three distinct groups of *L. venusta* webs, based on the number of spirals/web and principally on the height at which the webs were located; most *L. venusta* webs (63/100) were close to the ground. Spiders on high webs (153.8 ± 3.6 cm above ground, mean \pm S.E.) were significantly larger and heavier than spiders on lower webs. Large spiders had significantly larger, better developed ovaries, than smaller conspecifics, presumably indicative of sexual maturity. Significantly more insects were captured by sticky traps placed at 50 cm height than in the traps placed at 150 cm height; the most numerous captures were Diptera. However, insects caught at 150 cm were significantly larger than those caught at 50 cm above ground. We concluded that as sexual development proceeds, the spider increases the height at which the web is constructed. This vertical migration is associated with changes in web construction and the type of prey captured. These results are discussed in terms of intraspecific competition, predation risks and sexual selection.

Keywords: Web-building, prey, predation strategy, web location

During foraging, a predator has to make several choices: where to eat, how much time to dedicate to eating, and what type of prey to select for capture and consumption. These choices depend on strategies allowing the predator to optimize its behavioral efficiency and to reduce energetic costs and time (Alcock 1993).

Orb-weaving spiders are generalist predators that do not usually compete with each other for food (Wise 1993). This absence of competition may be a result of different species using different predatory strategies. Olive (1980) asserted that the functional morphology of the predator may directly affect the type of insect predated, as a means to avoid catching the same prey. One such strategy consists of reducing competition by building webs that differ in structure and location. In this way, each spider species produces one type of web and employs it in one type of micro-habitat (Hénaut et al. 2001). Alternatively, the web can act as a general filter and trap a large diversity of insects, and if the web is constructed at different sites, it can capture different

kinds of prey. For example, *Gasteracantha cancriformis* (Linnaeus 1785) builds a web in open areas whereas *Cyclosa caroli* (Hentz 1850) traps insects in the same type of habitat but only in enclosed areas (Ibarra-Núñez et al. 2001). In this case, selection of different prey items is achieved by a combination of differences in web location and spider behavior (Hénaut et al. 2001). These studies indicate that each spider species may adopt a particular strategy based on a combination of web characteristics, web location and spider behavior.

Leucauge venusta (Walckenaer 1841) is a common species in many habitats from the United States to South America (Levi 1981). In the field, *Leucauge* species generally spin inclined orb webs. The first web of the day is usually built before dawn and may be repaired or replaced during the day (Eberhard 1988). The usual sequence of orb-building is to make radii and frame lines, then hub loops followed by a temporary spiral, and finally the sticky spiral. The temporary spiral is used as a bridge when moving from one radial thread to the

next during construction of the sticky spiral (Eberhard 1987). *Leucauge venusta* is extremely abundant during the rainy season in coffee plantations in Chiapas State, Mexico (Pinkus-Rendón pers. comm.). The web of this species is constructed in semi-open sites generally between weeds or between adjacent coffee bushes (Ibarra-Núñez & Lachaud 1998).

The objective of the present study was to determine whether a relationship exists between the body size of the female spider or characteristics of the available prey, caught by sticky traps, and the structure and placement of *L. venusta* webs in a coffee plantation in the south of Mexico.

METHODS

Field observations.—The field site was a coffee plantation in the grounds of the INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias) agricultural experimental station at Rosario Izapa located at 400 m above sea level, approximately 15 km from the town of Tapachula (Chiapas, Southern Mexico) and 1 km from the border with Guatemala (14° 58' N, 92° 09' W). The climate is tropical; warm and humid with a typical daily temperature range of 35 °C maximum and 23 °C minimum, and a relative humidity of approximately 85%. Heavy rainfall occurs during the months of May to October (~300 mm/month) causing a marked reduction in spider activity in the field. The field collection occurred between October and November (2000), at the beginning of the dry season.

Adult female spiders were collected by walking between coffee plants (around 2 m height) in a 1000 m² area of the coffee plantation at intervals of six days. The characteristics of each web were recorded for each spider collected until a total of 100 spiders and webs had been sampled. Collections were performed early in the morning when the webs were still clean and undamaged. Voucher specimens of *L. venusta* collected were deposited in the entomological collection of El Colegio de la Frontera Sur (ECOSUR).

Characteristics of the web.—Web characteristics were measured directly in the field before collecting the corresponding occupant. We recorded the height (in cm) from the soil surface to the center of the orb and to the lowest and highest points of the web, the web diameter (in cm), the number of radii and the number of sticky spirals (from the centre to the bottom of the orb and from the centre to the lower point).

Spider characteristics.—The occupant of each web was collected alive in a tube and taken back to the laboratory where body length (in mm), abdomen width (in mm) were measured with binocular microscope and dry weight (in mg) of each spider was recorded. To determine the dry weight,

spiders were placed in aluminium foil, killed by freezing at -6 °C them 2 min and dried for 2 h in a temperature of 60 °C in an oven. An electronic balance was used to determine the weights (Sartorius Basic model BA 110S). In November, 30 spiders were collected randomly and the abdomen and ovary width were measured to determine whether a relationship existed between abdomen size and the development of the ovary. To measure the ovary size, ovaries were dissected out and the width measured using a binocular microscope at the widest point of the dissected ovary

Prey trapping.—To determine the abundance of different types of potential prey, 12 sticky traps were hung from randomly-selected coffee plants in the experimental area for periods of 2 days. Traps were located at 50 cm or 150 cm height above the ground and consisted of a transparent plastic board (30 × 20 cm) coated with Tangle Foot ©(The Tangle Foot Company, Grand Rapids MI 49504 USA) similar to those used by Eberhard (1977) and Uetz et al. (1978). Six traps were used for each height. Trapped insects were preserved in 70% ethanol and identified to order in the laboratory. Body size (length and width in mm) of each insect was also recorded as the maximum distance between head and the posterior tip of the abdomen and the maximum width of the thorax.

Statistics.—Principle Component Analysis was applied to determine the factors (web and spiders characteristics) that may separate different groups of spiders inside the study area. Web characteristics, body weight, body length and abdomen width of the spiders of the different groups were compared by Kruskal-Wallis test. The relationship between abdomen width and web characteristics of all the spiders was analysed by a non-parametric Spearman rank order correlation. The size of insects trapped at each height was compared by Mann-Whitney U test, whereas the numbers of insects of each order trapped at each height were compared using contingency tables (χ^2 test). The relationship between abdomen and ovary width was subjected to linear regression analysis.

RESULTS

Analysis of web and spider characteristics.—Principal component analysis clearly identified the presence of three distinct groups of *L. venusta* webs (Fig. 1). The first group was numerous with 63 webs, the second group had 18 webs and the third group represented 19 webs (Table 1). The height of webs above the ground increased significantly from an average (\pm S.E.) of 54.5 \pm 1.8 cm in group 1 to 153.8 \pm 3.6 cm in group 3 ($F = 363$, $d.f. = 2,97$, $P < 0.001$). In contrast, the number of spirals/web was negatively correlated with web height ($F = 5.6$, $d.f. = 2,97$, $P = 0.004$). Web diameter and the number of radii were statistically similar among the

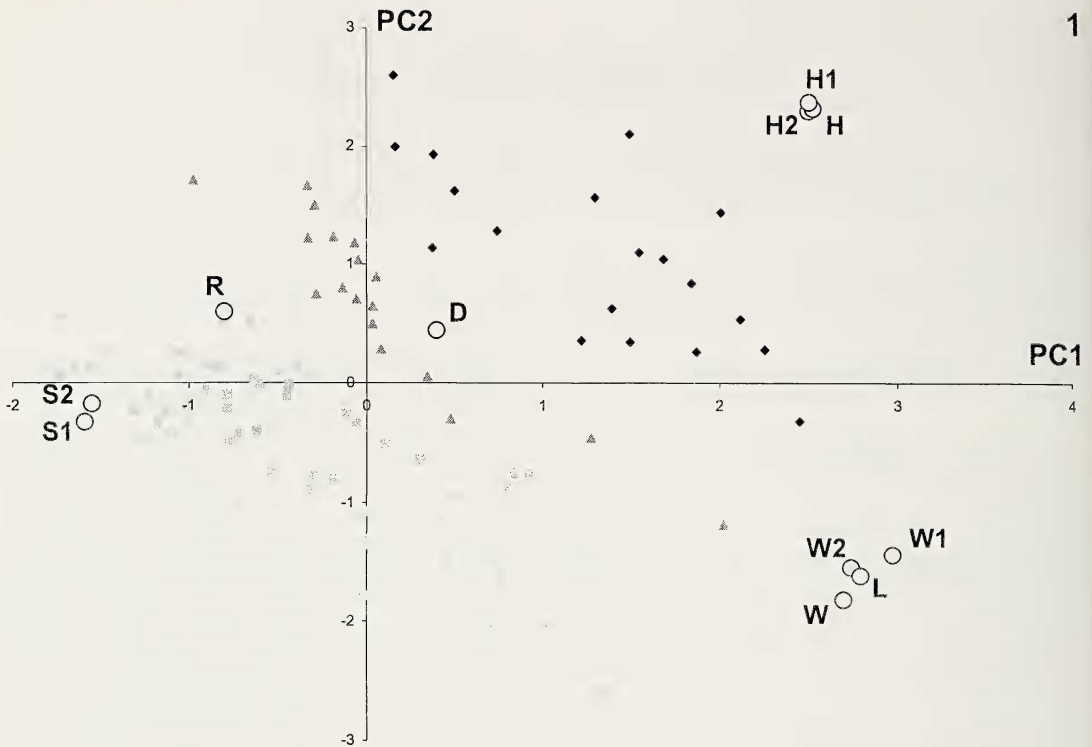


Figure 1.—Principle component analysis ($n = 100$) applied to the height of webs (H, H1, H2), web diameter (D), number of radii (R) per web, number of spirals (S1, S2), live weight (W1), dry weight (W2), body length (L), and abdomen width (W). We distinguished three spider groups (circles, triangles, squares). The first axis (PC1) explains 41% of the distribution and the second axis, (PC2) explains 21% of the distribution.

three groups (Table 1). The height at which the webs were located appears to be the principal factor separating the three groups; most *L. venusta* webs (63/100) were close to the ground.

The characteristics of the spiders also differed between the three groups of webs (Table 2). Spiders from web groups 1 and 2 were similar in weight (13.4–13.8 mg) whereas group 3 spiders were significantly heavier with an average dry weight of 17.3 ± 1.3 mg ($F = 3.45$, $d.f. = 2$, 97 , $P = 0.03$). A similar relationship was also detected with body length ($F = 3.55$, $d.f. = 2$, 97 , $P = 0.03$) and abdomen size ($F = 3.66$, $d.f. = 2$, 97 , $P = 0.02$);

group 3 spiders were larger than spiders from group 1 and group 2 webs in all respects.

Significant positive correlations were detected between *L. venusta* abdomen width and height of webs (Spearman = 0.2, $t(98) = 2.3$, $P = 0.02$), and abdomen width and number of web spirals (Spearman = -0.2, $t(98) = -2.5$, $P = 0.01$). The diameter of the web (Spearman = 0.07, $t(98) = 0.7$, $P = 0.5$), and the number of radii (Spearman = -0.1, $t(98) = -1.2$, $P = 0.2$), were not significantly correlated with abdomen width.

There was a significant positive correlation detected between abdomen size and ovary size ($F =$

Table 1.—Height, size and structural characteristics of three groups of *L. venusta* webs collected in Chiapas, Mexico during the rainy season of 2001. Figures represent means \pm SE. *** Mann-Whitney U-test, $P < 0.001$; ns, Not significant $P > 0.05$.

	Group 1 ($n = 63$)	Group 2 ($n = 18$)	Group 3 ($n = 19$)	<i>P</i>
Height of web (cm)	54.5 ± 1.8	101 ± 2.3	153.8 ± 3.6	***
Web diameter (cm)	29.1 ± 0.6	31.8 ± 1.4	30.1 ± 1.0	ns
Number of radii	34.7 ± 0.4	35.1 ± 1.0	35.2 ± 0.9	ns
Number of spirals	52.2 ± 1.0	47.0 ± 1.9	45.7 ± 2.2	***

Table 2.—Body weight, length and abdomen width of spiders collected from the three groups. All values are means \pm SE. Mann-Whitney U-test: * $P < 0.05$.

	Group 1 ($n = 63$)	Group 2 ($n = 18$)	Group 3 ($n = 19$)	P
Weight (mg)	13.4 \pm 0.6	13.8 \pm 1.2	17.3 \pm 1.3	*
Body length (mm)	5.6 \pm 0.7	5.58 \pm 0.1	6.1 \pm 0.1	*
Abdomen width (mm)	2.9 \pm 0.05	2.85 \pm 0.1	3.2 \pm 0.09	*

22.3, $d.f. = 1, 12, P < 0.001$, Pearson's correlation coefficient = 0.8); larger spiders had larger, better developed ovaries, presumably indicative of sexual maturity (Fig. 2).

Insects trapped.—Significantly more insects were captured in the traps placed at 50 cm height ($n = 225$) than in the traps placed at 150 cm height ($n = 150$) ($\chi^2 = 14.99, d.f. = 1, P < 0.001$). The majority of arthropods captured were Diptera (207), Hymenoptera (68) or Coleoptera (55), other arthropods found on traps included Homoptera (17), Hemiptera (2) Acari (13) and Araneae (13) (Table 3). As Diptera, Hymenoptera and Coleoptera were obviously the most common (88% of the trapped arthropods), we used these three groups for analysis.

A similar number of Hymenoptera and Coleoptera were caught on traps at 50 cm and 150 cm height ($\chi^2 = 2.1, d.f. = 1, P = 0.1$ for Hymenoptera; $\chi^2 = 1.4, d.f. = 1, P = 0.2$ for Coleoptera). In contrast, many more Diptera were caught at 50 cm than at 150 cm height ($\chi^2 = 5.9, d.f. = 1, P =$

0.01) and they were much more numerous than other insects at both 50 cm ($\chi^2 = 75.4, d.f. = 2, P < 0.001$) and 150 cm height ($\chi^2 = 53.7, d.f. = 2, P < 0.001$) (Table 3).

However, body length ($U = 4165, P = 0.01$) and width ($U = 4210, P = 0.02$) of flies trapped at 150 cm height were greater than for flies trapped at 50 cm height (Figure 3). A similar relationship was seen in hymenopterans (body length $U = 373, P = 0.01$; body width $U = 371.5, P = 0.01$). In the case of Coleoptera, body length was greater in individuals trapped at 50 cm ($U = 243.5, P = 0.03$) but no significant difference was detected in terms of body width ($U = 350, P = 0.7$) (Fig. 3).

Discussion.—The spatial distribution of the *L. venusta* population in a coffee plantation was studied in relation to different factors including web characteristics, spider maturity and prey size. It was possible to distinguish three groups of spiders in relation to the height of their webs. The majority of webs were located close to the ground (at ap-

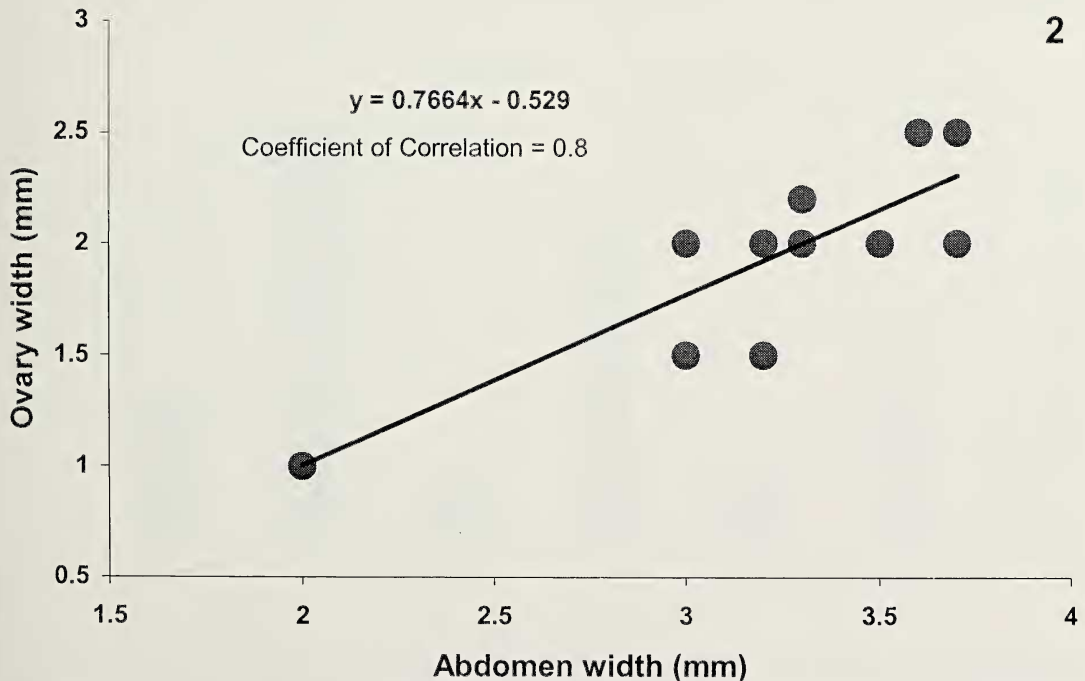


Figure 2.—Relationship between ovarian width and abdomen width ($P < 0.0001$) in *Leucauge venusta*.

Table 3.—Total number of prey trapped at two heights for the three principal groups of insects. χ^2 test: ** $P < 0.01$; *** $P < 0.001$; ns Not significant $P > 0.05$.

	50 cm height trap	150 cm height trap	<i>P</i>
Diptera	121	86	**
Hymenoptera	40	28	ns
Coleoptera	32	23	ns
Total	193	137	
<i>P</i>	***	***	

proximately 50 cm height), but a part of the population constructed webs at heights of ~100 cm or ~150 cm above the ground. Webs at different heights had similar diameters and number of radii but the number of spirals was reduced in webs at 150 cm height giving the webs a more open structure. Spiders occupying webs at ~150 cm were larger than conspecifics occupying lower webs. Body size was shown to be positively correlated with ovarian size in a sub-sample of these spiders.

Apparently, sexual development may influence the choice of web site. Web design may also be influenced by sexual development, or may be related to physical stresses experienced when webs are constructed high above the ground, such as air currents and movement of plant supporting structures. Traps placed at two different heights indicated that the majority of potential prey were dipterans and

that more insects were captured at 50 cm than at 150 cm height. Diptera and Hymenoptera, the preferred prey of *L. venusta* (Hénaut et al. 2001), caught at 150 cm height were, however, significantly larger than those caught at 50 cm height. Chacón and Eberhard (1980) found similar results using artificial webs: smaller insects were most frequently caught in the lowest traps. Ibarra-Núñez et al. (2001) also reported that the most common insects caught in *Leucauge* spp. webs are Hymenoptera and Diptera, and that Coleoptera were not important prey items.

The web location appears related to the sexual development of the spider. Observations in the field confirmed that *L. venusta* nymphs build webs close to the ground and that immature spiders may be very abundant (Pinkus-Rendón pers.comm.). Our results suggest that young adult spiders also build webs close to the ground, but as sexual development proceeds, the spider increases the height at which the web is constructed. This vertical migration is also associated with changes in web construction and the type of prey captured, with the possible effect of reducing intraspecific competition between *L. venusta* adults and juveniles. Another possibility is that sexually maturing spiders seek the larger prey that can be caught at higher sites in and between plant canopies. In the same way, a more open web structure with a larger mesh size may be an adaptation to target the capture of larger prey, as reported in *Argiope* species (Uetz et al. 1978). Uetz and Hartsock (1987) found that webs of *Micrathena gracilis* (Walckenaer 1805) show selectiv-

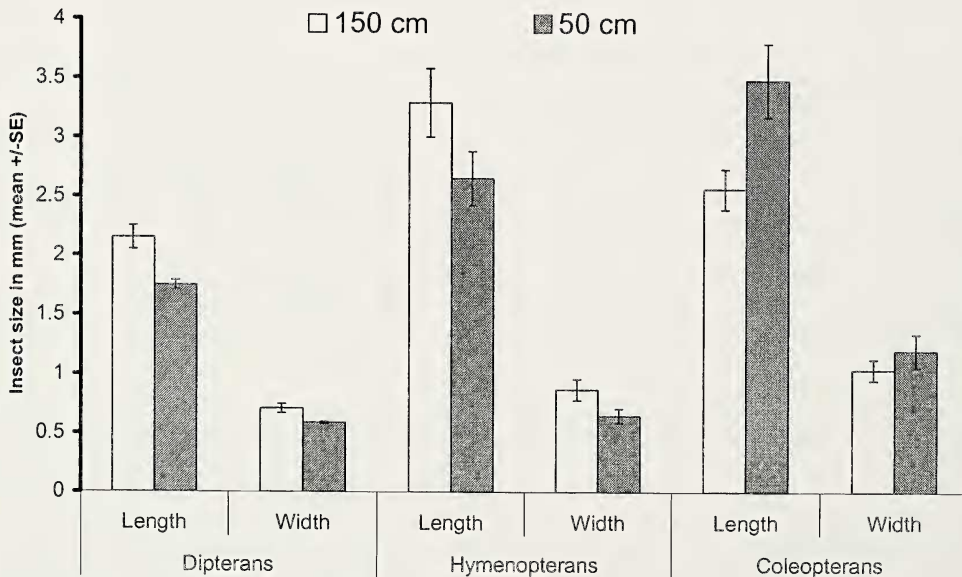


Figure 3.—Comparison of body length and width of Diptera, Hymenoptera and Coleoptera caught on sticky traps placed at 50 and 150 cm above the ground in a coffee plantation (Mean \pm SE). Mann-Whitney U test: * $P < 0.05$, ** $P < 0.01$, ns Not significant $P > 0.05$.

ity for prey sized greater than 3 mm even if potential prey are smaller. The same phenomenon of prey specialization may be also occur in *L. venusta* and in this case be reinforced by web relocation.

The dynamics of habitat choice in spiders are complex and difficult to analyze. Spider behavior represents a compromise between many needs during the life cycle and the choices available may often be limited (Riechert & Gillespie 1986). Spatial distribution may be influenced by the competition for suitable web sites. Dispersal can occur on two levels, first haphazardly by ballooning on air currents followed by a controlled and active site selection (Riechert 1970). This active dispersal has been described by Kronk and Riechert (1979) wherein, similar to the results of our study with *L. venusta*, the sexual maturity of females induces migration to sites in which prey are more abundant.

There are, however, alternative interpretations of these results. First, larger spiders may exclude smaller conspecifics from high locations by aggression (Danielson-François et al. 2002). Second, larger spiders that spin looser webs higher in the coffee canopy may also competitively exclude smaller spiders that construct webs with closer spirals. Third, predatory wasps may also influence the vertical distribution of spiders; larger spiders experience a significantly diminished risk of predation (Blackledge & Wenzel 2001). Finally, the vertical migration during the search for females could be a serious constraint upon male mating success in orb weaving spiders (Moya-Laraño et al. 2002). This suggests that female *L. venusta* may migrate upwards as a means of selecting especially vigorous males as mates.

In conclusion, the variability in web construction in *L. venusta* is correlated with sexual maturity and predatory opportunities perhaps dictated by the energy required for the development of eggs and reproductive activities. Constructing an open web in a site with an abundance of large prey may represent savings in terms of silk production and a reduction in intraspecific competition with immature conspecifics. These observations illustrate how web site selection may reflect physiological needs associated with spider reproduction in habitats with heterogeneous predation opportunities.

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